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Invertebrate diversity associated with tropical mistletoe in a suburban landscape from northern Australia

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Abstract

The invertebrate fauna associated with the tropical mistletoe *Decaisnina signata* (Loranthaceae) parasitising a range of host trees was surveyed during the late dry-season (September-October) in suburban areas of Darwin, Northern Territory, a landscape which comprises extensive patches of natural vegetation within the urban matrix. A total of 113 species of insects and spiders representing 51 families and 12 orders was recovered from 38 samples. The estimated total species richness, however, suggests another 116 species are likely to occur on the mistletoe according to the incidence-based coverage estimator (ICE). Hymenoptera (especially Formicidae), Hemiptera (particularly Miridae), Araneae and Lepidoptera were the most dominant groups in our samples in terms of both species richness and relative abundance (measured as % site occupancy). Thysanoptera, Coleoptera and Psocoptera were also comparatively diverse but were substantially less abundant. Overall species and family richness were both positively correlated with mistletoe biomass, but the composition and taxonomic richness of invertebrates associated with mistletoes parasitising different host genera (*Planchonia* vs. *Alstonia*) or host species (*Alstonia scholaris* vs. *A. actinophylla*) were not significantly different. Our findings are in broad agreement with limited previous studies elsewhere that indicate mistletoes support a wide range of invertebrates, some of which are obligate specialists. We hypothesize that mistletoes support a unique assemblage of invertebrates that is independent of the host tree.

Introduction

Mistletoes are a functional group of aerial-stem hemiparasitic plants in the plant order Santalales. Most mistletoes selectively parasitise trees and shrubs in forests and woodlands (Calder & Bernhardt 1983) and it has been demonstrated that the arboreal parasitic habit has arisen independently five times, in the families Misodendraceae, Loranthaceae, Santalaceae, 'Santalaceae' (Amphorogyneae) and Viscaceae (Vidal-Russell & Nickrent 2008). Watson (2001) concluded that mistletoes represent a critical keystone resource in these habitats worldwide because they support high biodiversity and facilitate numerous complex ecological interactions, including pollination, frugivory and herbivory. Mistletoes have also been found to increase ground litter mass and plant productivity, measured in terms of understorey plant biomass (March & Watson 2007).

Although birds and to some extent mammals use mistletoes as a resource for food and breeding sites (Reid 1987; Watson 2001; Cooney *et al.* 2006), there has been comparatively little research on insect communities associated with mistletoes world-wide. Perusal of the literature indicates that, at the species level, insects regularly feed on mistletoes, including the nectar of flowers (Barlow 1966; Stevens & Hawksworth 1970; Bernhardt & Calder 1981; Nickrent 1988), the woody tissue of the haustorium, stems or dead branches (Miller & Keen 1960; Room 1972a; Hawkeswood & Peterson 1982; Whittaker 1984, De Baar 1985a,b; Williams 1985; McMillan 1987; Common 1990), and the leaves, non-woody stems, fruits or flowers (Watt & Casimir 1962; Stevens & Hawksworth 1970; Room 1972a; Whittaker 1984; Scharpf & Koerber 1986; De Baar 1985a,b; Common 1990; van Harten 1996; Patrick & Dugdale 1997; Taylor 1999; Braby 2000, 2005, 2006; Lane & Edwards 2005; Braby & Nishida 2007). In addition, they may serve as effective pollinators of mistletoes (Barlow 1966; Stevens & Hawksworth 1970; Penfield *et al.* 1976; Bernhardt & Calder 1981; Kelly *et al.* 1996; Ladley *et al.* 1997; Nickrent 1988; Robertson *et al.* 2005). Moreover, several observations suggest complex interactions amongst the various insect feeding guilds. For example, Room (1972b) noted that wood borers (Coleoptera and Lepidoptera) provide holes for mealy bugs (Homoptera), which are attended by large numbers of ants (Hymenoptera) to obtain honeydew; the ants in turn appear to provide protection to the mistletoe by reducing attack from insect herbivores. In Australia, wood-boring beetles such as the weevil *Metyrus albicollis* Germ. (Coleoptera) create tunnels inside the haustorium and woody branches of mature clumps of *Amyema* (De Baar 1985a,b; McMillan 1987); ants of the genus *Froggattella, Crematogaster* and others such as *Tetraponera* frequently establish nests inside the tunnels, which are also used as convenient shelters by larvae of some species of *Ogyris* (Lepidoptera) which have an obligate relationship with the ants (Eastwood & Fraser 1999).

Interestingly, while there are numerous examples in the literature of insects feeding obligatorily on mistletoes, there are relatively few cases of lineages radiating adaptively on mistletoes. For example, in the Lepidoptera only four instances of adaptive radiation are known: in the subtribe Aporiina (Pieridae) from Africa, Asia-Australia and South America (Braby 2005, 2006; Braby & Trueman 2006; Braby *et al.* 2007; Braby & Nishida unpubl.); in the *Hesperocharis* group of the tribe Anthocharidini (Pieridae) from Central and South America (Braby & Nishida 2007); in the tribe Iolaini (Lycaenidae) from Africa (Congdon & Bampton 2000); and in the tribe Ogyrini (Lycaenidae) from Australia (Braby 2000).

While there is clearly an extensive literature documenting insects and other invertebrates associated with mistletoes, there are remarkably few studies that describe the invertebrate assemblage as a whole and the spatial and/or temporal patterns of these communities for particular mistletoe taxa. A detailed review of *Arceuthobium* (Viscaceae) in the western USA and Mexico indicated a rich and varied arthropod fauna associated with the genus (Stevens & Hawksworth 1970). Room (1972a) undertook a comprehensive survey of the invertebrate fauna associated with *Tapinanthus bangwensis* (Engl. & K.Krause) Danser (Loranthaceae) from Ghana in tropical West Africa and recorded over 610 species from the branches and leaves, and more than 440 species from the haustorium and hypertrophied host tissue, representing 18 orders from the Crustacea, Insecta, Arachnida and Mollusca. In terms of species richness, the most dominant orders sampled were Araneae, Hymenoptera, Coleoptera, Lepidoptera and Hemiptera. Whittaker (1984) provided a detailed inventory of the temperate insect fauna on *Phoradendron tomentosum* Engelm. ex A.Gray (Viscaceae) from southern Texas, USA; between spring and mid autumn 43 species of insects were recorded, of which the Hymenoptera, Hemiptera, Coleoptera and Lepidoptera were the most diverse.

The aim of this study is to describe the spider and insect assemblage associated with the tropical mistletoe *Decaisnina signata* (F.Muell. ex Benth.) Tiegh. (Loranthaceae) within a suburban landscape during the late dry-season, as part of a broader survey to document the invertebrate diversity of mistletoes in northern Australia. In addition, we compare the composition and taxonomic richness of invertebrates recorded on *D. signata* parasitising two distantly related host tree genera (*Planchonia* vs. *Alstonia*) and two closely related host tree species (*Alstonia scholaris* vs. *A. actinophylla*) to establish if host tree affects diversity. If it is assumed that mistletoe invertebrate diversity is dependent on the host tree, then our prediction is that the mistletoe-invertebrate fauna will be different among host tree categories because the hosts are distantly related taxonomically and therefore likely to support different faunas that colonise or interact with mistletoes. Moreover, *Alstonia* (Apocynaceae) has milky white sap containing alkaloids and other toxic compounds (e.g. Arulmozhi *et al.* 2007; Oigiangbe *et al.* 2007), which are known to deter insect herbivores and sap-suckers, so one might predict that such host trees harbour a more specialised fauna that colonises mistletoes compared with that associated with *Planchonia* (Lecythidaceae), which does not contain these compounds.

Methods

Study species

Decaisnina includes six species in the monsoon tropics of northern Australia, of which four occur in the Northern Territory (NT). *Decaisnina signata* (Figure 1) is endemic to the Kimberley, WA, and the Top End of the NT (Barlow 1993), and is the predominant species of the genus in the Darwin region (Dunlop *et al.* 1995). It has spectacular, showy red flowers and occurs in both monsoon forests and savanna woodlands (Barlow 1993). It is well established in suburban areas of Darwin (Figure 1) where its main hosts are species of *Planchonia, Alstonia, Eucalyptus, Melaleuca* and *Syzygium* (Clark & Traynor 1987); Barlow (1993) and Downey (1998) listed several other native genera on which it grows. *Decaisnina signata* is the most abundant mistletoe within Darwin, in part due to its ability to parasitise a wide range of both native and ornamental host trees. It is known to serve as a larval food plant for the butterflies (Lepidoptera) Scarlet Jezebel *Delias argenthona* (Fabricius) (Wade 1978), Northern Pencil-blue *Candalides margarita gilberti* Waterhouse (Samson & Wilson 1995) and Northern Purple Azure *Ogyris zosine* (Hewitson) (Braby 2000). For these reasons, *D. signata* was chosen as our preferred study species.

Figure 1. (A) Suburban habitat in Darwin, NT, showing the ornamental host tree *Alstonia scholaris* supporting clumps of the study mistletoe *Decaisnina signata*; (B) habitus of *D. signata* parasitising *A. scholaris* (inset photo shows inflorescence of *D. signata*).

Study area and host trees

In order to describe the invertebrate fauna associated with *Decaisnina signata*, 38 sites (i.e. mistletoe clumps) were selected throughout the suburbs of Darwin, NT (Figure 2). All sites were located either in urban areas (usually on road nature strips or near footpaths), or in suburban parklands associated with cleared or disturbed vegetation. No sites were located in areas comprising natural vegetation, although several were close to small patches of natural habitat.

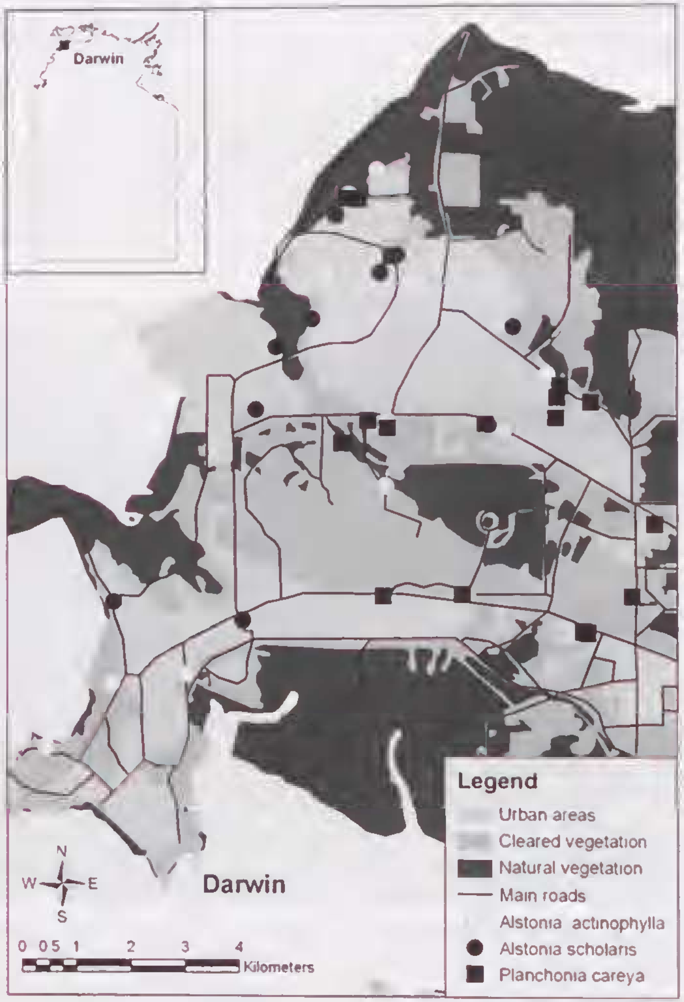

Figure 2. Map of study area showing sampling sites in the Darwin district (inset map shows Northern Territory and location of Darwin). Host trees for each site are indicated in the legend.

To test for host tree effects on invertebrate diversity, mistletoe clumps parasitising two distantly related host genera were sampled: Cocky Apple *Planchonia careya* (F.Muell.) R.Knuth (Lecythidaceae) (18 sites) and *Alstonia* (Apocynaceae) (20 sites). Within the *Alstonia* host trees, two species were compared: Cheesewood or Milky Bean *A. scholaris* (L.) R.Br. and Milkwood *A. actinophylla* (A.Cunn.) K.Schum., with ten mistletoe sites sampled for each. *Planchonia careya* naturally occurs widely across the monsoon tropics of northern Australia and is a common understorey tree growing 4-10 m high in open-forest and woodland. It is semi-deciduous or deciduous during the mid dry-season (July-August) when trees frequently shed most or all of their leaves. Of the two species of *Alstonia* in the Darwin region, only *A. actinophylla* is indigenous; it occurs naturally in open-forest and woodland, but also in monsoon forest (semi-deciduous coastal monsoon vine-thicket, monsoon vine-forest), where it grows as a large evergreen tree 15-20 m high with a spreading crown and thick short trunk. *Alstonia scholaris* was introduced to the Darwin region as an ornamental street tree (Figure 1); it occurs naturally in Queensland where it grows as an emergent tree (>10 m) in rainforest. All three host trees are readily parasitised by *D. signata*, and on some trees, especially plants growing in more exposed situations or the non-indigenous species *A. scholaris,* infestations may reach exceedingly high levels.

Sampling

Invertebrates were sampled during the late dry-season (September-October 2006) between 0600-1100 h (i.e. during calm, dry, sunny weather). The number of mistletoe clumps on each host tree was recorded. Where two or more mistletoe clumps occurred on a host tree, only one clump was sampled, generally that which was accessible by foot or ladder. Mistletoe clumps touching the ground or those near the canopy of the host tree were not sampled to avoid possible loss of invertebrates during sampling. Because of the potential negative impact of Green Tree-ants *Oecophylla smaragdina* (Fabricius) (Hymenoptera: Formicidae) on invertebrate diversity, clumps with colonies of this predacious ant species were avoided.

Clumps of mistletoes were enclosed in 75 L plastic bags, removed from the host tree at their point of attachment, weighed, and then transferred to a freezer (-10°C). After 24 h, invertebrates were removed from each sample as follows. Branches were broken into approximately 250 mm lengths, placed in a 5 L container and submerged in 150 mm of water. Leaves, flowers, fruits, buds and stems were inspected visually for invertebrates, with the woody parts broken into 50 mm lengths to isolate borers. The collection bag was then submerged in a separate container of water to remove additional invertebrates. Contents of both containers were filtered through a 0.025 mm polyester sieve; after filtering, invertebrates were flushed with 70% ethyl alcohol. All invertebrates were removed, sorted and preserved in vials with 70% ethyl alcohol.

The destructive sampling method was found preferable over other methods. An alternative method of enclosing the mistletoe clump inside a large plastic bag and spraying with pyrethrum-based insecticide and shaking the foliage to dislodge invertebrates (A. Burns, pers. comm.), was not suitable as it caused larvae and other small insects to adhere to the leaves and stems. Difficulty was experienced in identifying Lepidoptera larvae to family level regardless of the sampling method adopted. To overcome this, samples of larvae (where sufficient duplicates were available) were kept alive and reared to adulthood in small plastic containers (160 mm x 110 mm x 80 mm) supplied with fresh cuttings of leaves and/or flowers.

Invertebrates (spiders and insects) were identified to the level of order and family. With the exception of thrips (Thysanoptera), moths and butterflies (Lepidoptera) and ants (Hymenoptera: Formicidae), lower taxa were not identified to species level, but were distinguished on the basis of clear morphological differences (i.e. morphospecies). The following works were consulted to assist with routine identifications: CSIRO (1991), Rentz (1996), Andersen (2000), Braby (2000), Brunet (2000), Cassis *et al.* (2002), Lawrence *et al.* (2000), Raven *et al.* (2002), Zborowski and Storey (2003), Horne and Crawford (2005) and Grimaldi and Engel (2005).

Statistical analyses

Species accumulation curves and species richness were estimated using Version 8.0.0 of the EstimateS software program (Colwell 2006). The program computes the expected species richness (Mao Tau) for a given set of samples, as well as the incidence-based coverage estimate (ICE), to determine total species richness.

To detect patterns of similarity in species composition of invertebrates among mistletoe clumps growing on different host trees (three levels), multivariate analysis employing an ordination method based on semi-strong hybrid multidimensional scaling (SSH MDS) was implemented using PATN v3.03. Bray-Curtis similarity measure was applied to the data set (species by sites) to create a symmetric diagonal matrix of similarities, analogous to correlation coefficients ranging from 0 (indicating that sites are different, with no species in common) to 1 (sites are similar, with all species in common) with a cut-off point of 0.01. The approach of using presence/absence data was preferred over using abundance data because of the high proportion of singletons and the fact that abundances varied greatly between life stages within species (e.g. larvae/nymphs were more abundant than adults). The three host tree levels tested were *Planchonia careya*, *Alstonia scholaris* and *A. actinophylla*.

Taxonomic richness was analyzed at two levels, species and family, using Stata v8.2. Parametric methods were used because species and family richness across sites were both found to be normally distributed (Shapiro-Wilk W test). Initial inspection of the data revealed that taxonomic richness was positively related to plant biomass (i.e. fresh weight) so mistletoe weight was included to control for biomass. Therefore, to test for possible differences among invertebrates on mistletoe clumps growing on different host trees, taxonomic richness (dependent variable) was analysed using one-way analysis of covariance (ANCOVA), with MISTLETOE WEIGHT as the covariate. For each level of taxonomic richness, two analyses were performed on the independent variable host tree, each with two categories. First, host tree was analysed at the generic level HOST TREE GENERA, with the two categories being *Planchonia* and *Alstonia*. Second, within *Alstonia*, host tree was analysed at the specific level HOST TREE SPECIES, with two categories: *A. scholaris* and *A. actinophylla*. Because of the small sample sizes (only 10 samples for each category of HOST TREE SPECIES treatment were tested), a stringent standard for testing of significance ($P < 0.01$) was adopted, thereby minimising the risk of type I errors.

Results

Composition

Table 1 provides a summary of the higher taxonomic groups at the ordinal and familial levels, number of morphospecies and relative abundance, given as the percentage site occupancy or frequency of occurrence across sites. A more detailed list summarising the species by site data for each sample is given in the Appendix. In total, 113 species of invertebrates representing 12 orders and 51 families were recorded on *Decaisnina signata*. An additional nine species from five orders were recorded but could not be accurately identified to family level. Hymenoptera (29 species, 11 families), Hemiptera (16 species, 8 families), Coleoptera (11 species, 5 families), Araneae (11 species, 3 families), Thysanoptera (11 species, 2 families), Lepidoptera (9 species, 6 families) and Psocoptera (9 species, 5 families) were relatively diverse in terms of taxonomic richness at the species level, whereas Neuroptera (3 species, 3 families), Collembola (1 species) and Mantodea (1 species) were relatively poor at both taxonomic levels (Table 1). The remaining two orders (Diptera, Blattodea) were, by comparison, moderately represented with seven and five species, respectively. In terms of relative abundance, the most frequently sampled taxa across sites were Araneae (97%), Hemiptera (92%), Hymenoptera (87%) and Lepidoptera (71%). Although Thysanoptera, Coleoptera and Psocoptera were relatively species rich, they were not abundant numerically (47%, 45%, 32% respectively). In contrast, Blattodea were relatively abundant (66%) but substantially less diverse. Diptera (16%), Neuroptera (13%), Collembola (3%) and Mantodea (3%) were sampled very infrequently. Hence, in terms of both species richness and relative abundance the most dominant groups in our samples were Hymenoptera (especially Formicidae), Hemiptera (particularly Miridae), Araneae and Lepidoptera (Table 1).

Plots of the cumulative number of species against the number of sites sampled give an indication of sampling effectiveness and whether all invertebrates were surveyed. Figure 3a shows that the accumulation curves were still increasing after 38 samples (all sites pooled), with no clear sign of reaching an asymptote. This trend is seen more clearly with ICE estimator in which the trajectory of the curve has not levelled off after the 38 samples, with a minimum mean estimated total species richness of 229 (Figure 3b). These estimates strongly indicate that the late dry-season invertebrate fauna was not fully surveyed, and that our overall sample represented about 49% of the total fauna. Despite these limitations, ordination of sites according to host tree genera and host species showed no clear separation of the data (Figure 4), indicating that the invertebrate composition was not significantly different among the host treatments.

Table 1. Taxonomic composition of invertebrates recorded at the ordinal and familial level on *Decaisnina signata*. For each taxonomic level, the number of morphospecies and relative abundance (% sites occupied, n = 38) are also given. See Appendix for further details.

Order	Family	No. of species	% sites occupied
Araneae	Salticidae	7	50.0
	Tetragnathidae	2	7.9
	Heteropodidae	1	2.6
	Unplaced	1	97.4
	Total	**11**	**97.4**
Collembola	Entomobryidae	1	2.6
Blattodea	Blattellidae	5	65.8
Mantodea	Mantidae	1	2.6
Psocoptera	Pachytroctidae	1	2.6
	Caeciliidae	1	5.3
	Ectopsocidae	2	10.5
	Archipsocidae	1	2.6
	Philotarsidae	1	2.6
	Unplaced	3	26.3
	Total	**9**	**31.6**
Thysanoptera	Thripidae	4	15.8
	Phlaeothripidae	7	47.4
	Total	**11**	**47.4**
Hemiptera	Aphididae	1	10.5
	Pseudococcidae	1	13.2
	Cicadellidae	2	31.6
	Tropiduchidae	1	15.8
	Flatidae	3	7.9
	Miridae	6	81.6
	Tingidae	1	2.6
	Pentatomidae	1	7.9
	Total	**16**	**92.1**
Diptera	Culicidae	1	2.6
	Ceratopogonidae	3	7.9
	Cecidomyiidae	1	2.6
	Sciaridae	1	2.6
	Sphaeroceridae	1	2.6
	Total	**7**	**15.8**

Table 1 continued

Order	Family	No. of species	% sites occupied
Coleoptera	Curculionidae	3	7.9
	Scolytidae	1	5.3
	Silvanidae	1	5.3
	Phalacridae	1	5.3
	Coccinellidae	2	15.8
	Unplaced	3	10.5
	Total	**11**	**44.7**
Neuroptera	Mantispidae	1	2.6
	Hemerobiidae	1	2.6
	Chrysopidae	1	7.9
	Total	**3**	**13.2**
Lepidoptera	Psychidae	2	5.3
	Immidae	1	13.2
	Pyralidae	1	28.9
	Geometridae	1	2.6
	Pieridae	1	2.6
	Lycaenidae	2	5.3
	Unplaced	1	31.6
	Total	**9**	**71.1**
Hymenoptera	Formicidae	11	68.4
	Chalcididae	1	2.6
	Pteromalidae	1	7.9
	Encyrtidae	4	13.2
	Agaonidae	1	7.9
	Scelionidae	4	34.2
	Aphelinidae	1	13.2
	Braconidae	2	10.5
	Bethylidae	1	2.6
	Eulophidae	1	2.6
	Elasmidae	1	2.6
	Unplaced	1	7.9
	Total	**29**	**86.8**

Taxonomic richness

The frequency distribution of species richness (Figure 5a) and family richness (Figure 5b) across sites indicated that the number of invertebrate species sampled per site varied from 3 to 17 ($\bar{x}$ = 10.3 ± 3.85 s.d.), while the number of families sampled varied from 2 to 12 ($\bar{x}$ = 6.8 ± 2.63 s.d.). Variation in taxonomic richness was found to be unrelated to the number of mistletoe clumps on host trees for both invertebrate species and families (r = 0.09, d.f. = 36, P > 0.10), but was positively correlated with mistletoe biomass (Figure 6). There was a highly significant linear relationship between mistletoe fresh weight and richness of both species (F = 16.30, d.f. = 36, P = 0.0003) and families (F = 11.68, d.f. = 36, P = 0.0016).

Mistletoe host tree had no effect on taxonomic richness, with similar numbers of invertebrate species (Figure 7a) and families (Figure 7b) recorded among the host tree categories. One-way ANCOVA, with MISTLETOE WEIGHT as the covariate, revealed no significant difference between invertebrate species richness on the HOST TREE GENERA *Planchonia* ($\bar{x}$ = 9.2 ± 1.06 s.e.) and *Alstonia* ($\bar{x}$ = 11.0 ± 0.80 s.e.) or between the HOST TREE SPECIES *Alstonia scholaris* ($\bar{x}$ = 10.5 ± 1.49 s.e.) and *A. actinophylla* ($\bar{x}$ = 11.5 ± 0.69 s.e.) at the $P < 0.01$ level (Table 2). Similarly, there was no significant difference in invertebrate family richness between *Planchonia* ($\bar{x}$ = 5.5 ± 0.62 s.e.) and *Alstonia* ($\bar{x}$ = 7.2 ± 0.60 s.e.), or between *Alstonia scholaris* ($\bar{x}$ = 7.3 ± 1.07 s.e.) and *A. actinophylla* ($\bar{x}$ = 7.0 ± 0.60 s.e.) (Table 3).

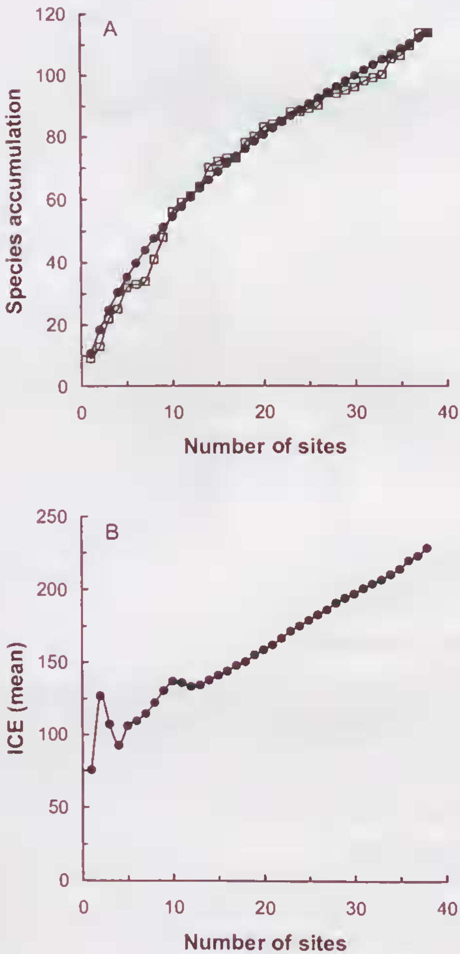

Figure 3.
Species accumulation curves and total predicted species richness curve based on incidence-based coverage estimator in relation to the number of mistletoes sampled (all sites pooled): (a) actual cumulative number of species (☐) and modeled species accumulation (Mao Tau) (●); (b) cumulative incidence-based coverage estimate (ICE).

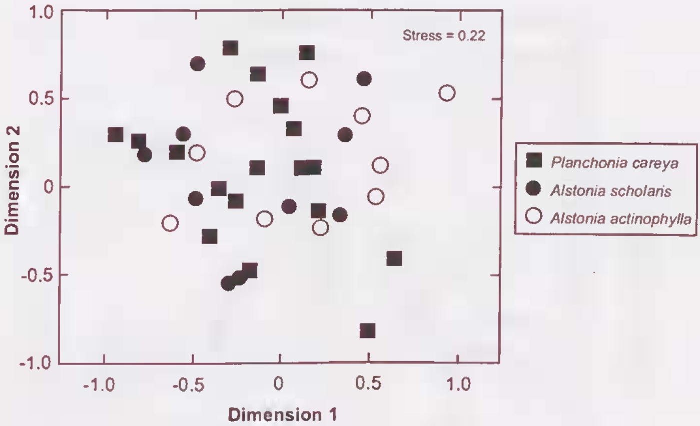

Figure 4. Multidimensional scaling ordination plot showing invertebrate composition associated with mistletoes parasitising three different host trees. Points represent Bray-Curtis similarity values based on presence-absence data (see Appendix for data).

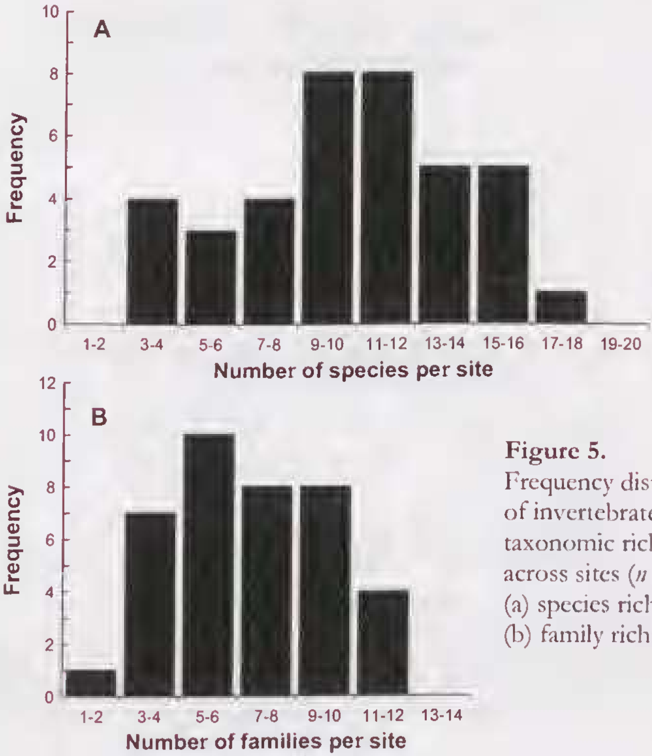

Figure 5. Frequency distribution of invertebrate taxonomic richness across sites (n = 38): (a) species richness; (b) family richness.

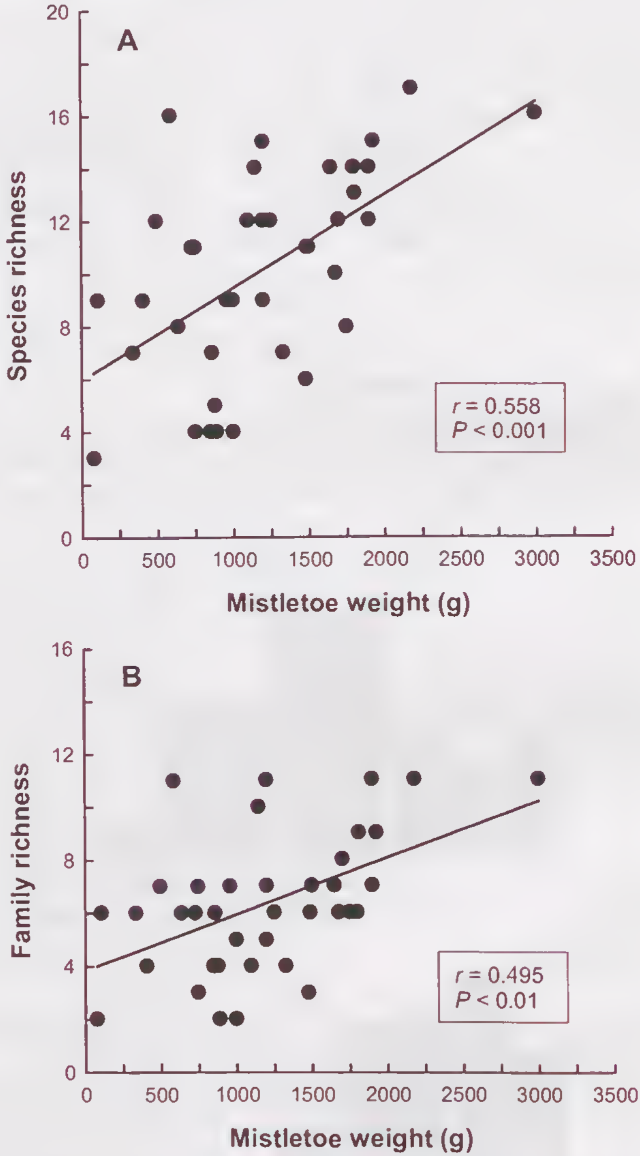

Figure 6. Relationship between invertebrate taxonomic richness and mistletoe fresh weight (all sites pooled): (a) species; (b) families. Regression equations: y = 0.0035x + 5.97 ($r^2 = 0.31$, $n = 38$) for species richness; y = 0.0021x + 3.84 ($r^2 = 0.24$, $n = 38$) for family richness.

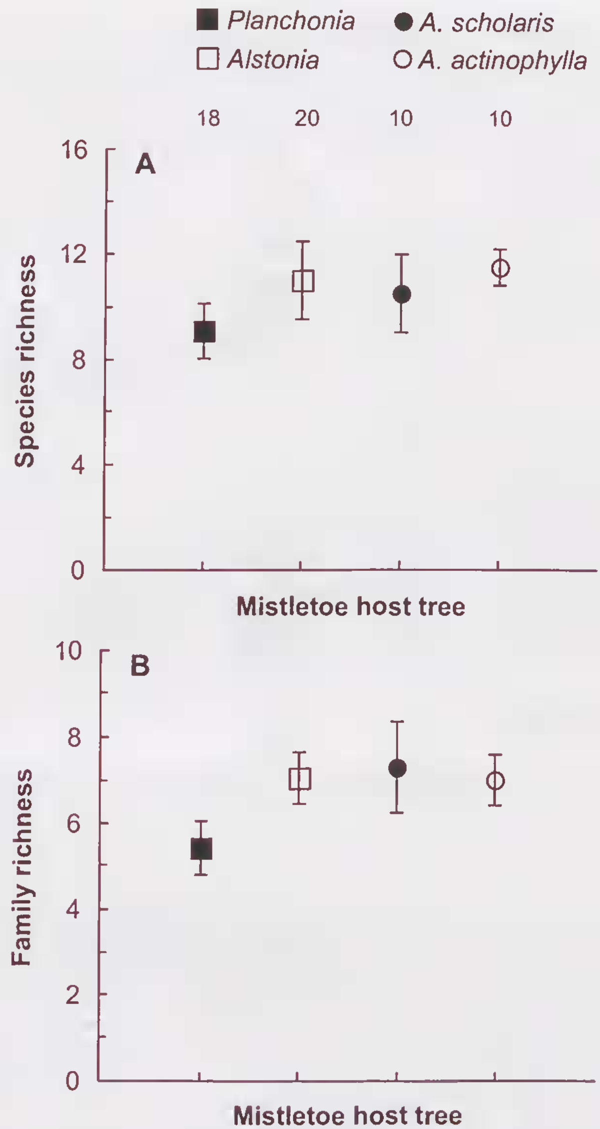

Figure 7. Invertebrate taxonomic richness (mean ± s.e.) recorded on mistletoe clumps parasitising different host tree genera (*Planchonia*, *Alstonia*), and different host tree species (*Alstonia scholaris*, *A. actinophylla*): (a) species richness; (b) family richness. Sample sizes are given above data points.

Table 2. One-way analyses of covariance of host tree genera (*Planchonia, Alstonia*) and host tree species (*Alstonia scholaris, A. actinophylla*) on invertebrate species richness, with mistletoe weight as covariate.

Source of variation	d.f.	MS	*F*	*P*
HOST TREE GENERA	1	13.6434	1.57	0.2183
MISTLETOE WEIGHT	1	98.1904	11.32	0.0019
Error	35	8.6727		
HOST TREE SPECIES	1	30.5274	4.79	0.0437
MISTLETOE WEIGHT	1	55.6251	8.73	0.0093
Error	17	6.3687		

Table 3. One-way analyses of covariance of host tree genera (*Planchonia, Alstonia*) and host tree species (*Alstonia scholaris, A. actinophylla*) on invertebrate family richness, with mistletoe weight as covariate.

Source of variation	d.f.	MS	*F*	*P*
HOST TREE GENERA	1	13.8706	3.46	0.0715
MISTLETOE WEIGHT	1	31.4828	7.86	0.0083
Error	35	4.0073		
HOST TREE SPECIES	1	2.3407	0.51	0.4871
MISTLETOE WEIGHT	1	27.8229	6.01	0.0260
Error	17	4.6263		

Discussion

A relatively diverse dry-season invertebrate fauna, comprising 113 morphospecies from 51 families representing 12 different orders, was recovered from the tropical mistletoe *Decaisnina signata* in the suburbs of Darwin. Moreover, the species accumulation curves and estimated total species richness, according to the incidence-based coverage estimator (Figure 3), show that the number of species is still increasing, indicating that our faunal inventory was incomplete. The ICE mean estimate was 229 species, which implies that only about half of the total fauna was sampled (i.e. a further 116 species are likely to occur on the mistletoe). These data are consistent with limited previous studies reported elsewhere in the world (Stevens & Hawksworth 1970; Room 1972a; Whittaker 1984) that show that mistletoes in both the Loranthaceae and Viscaceae support high numbers of invertebrates. The studies are not strictly comparable, because of differences in sampling intensity, seasonal timing and spatial area covered, but do serve to highlight the relatively large number and broad range of spiders and insects associated with mistletoes in both temperate and tropical habitats. Nevertheless, there are some striking similarities in invertebrate taxonomic composition. Hymenoptera, Hemiptera, Araneae and Lepidoptera were relatively dominant in our samples in terms of both taxonomic richness and relative abundance, a finding which is in broad agreement with those of Room (1972a) and Whittaker (1984).

Interestingly, a high proportion of the total species associated with *D. signata* (53%, $n = 60$) were rare, sampled from only a single site (Appendix), a finding that is similar to that of Room (1972a) who found that about two-thirds of all species collected from *Tapinanthus bangwensis* from Ghana were singletons. The large proportion of rare species associated with these two tropical mistletoes in northern Australia and West Africa parallels the general trend documented for tropical forests in which singletons are characteristic of herbivorous insect communities, often representing more than half of the species, even in large samples (Novotný & Basset 2000 and references therein). A proportion of these 'rare' taxa associated with *Decaisnina* are probably transient (incidental) or represent an artefact due to insufficient sampling. However, other rare species may either be distributed in relatively low population density across the suburban landscape (suffusive rarity) or have a highly clumped pattern of distribution that is patchier than the spatial distribution of the mistletoe (Calder & Bernhardt 1983). Alternatively, some rare species may be diffusively rare (Schoener 1987; Novotný & Basset 2000), comprising generalists that rarely feed on *D. signata* but which are more abundant across other more preferred host plant species, or specialists that occasionally use *D. signata* but are more numerous on other mistletoe species.

Our preliminary survey from the NT of northern Australia and surveys carried out in Ghana (Room 1972a), Pakistan (Baloch & Ghani 1980) and southern Texas, USA (Whittaker 1984) suggest that insects and other invertebrates associated with mistletoes can be divided into six broad functional categories: transient, facultative generalists, obligate specialists, predators/parasitoids, scavengers/detritivores and mutualistic associates. Transient species are incidentals or 'tourists' that come into contact with mistletoes irregularly and are not dependant on the mistletoe or its associated fauna as a resource. Facultative generalists are those species that feed upon or use the plant in some way (e.g. ants utilising tunnels made by wood boring larvae), but are not necessarily dependent on the mistletoe for survival because they can utilise resources from other plant families. Obligate specialists are those species that feed exclusively on mistletoes (i.e. wood, leaves, flowers, fruits) and are dependant on the resource for survival. Predators and parasitoids include those species that prey on (e.g. spiders) or parasitise (e.g. wasps) other insects on mistletoes, while scavengers and detritivores include species which feed on dead organic matter. Mutualistic associates include participants in beneficial interactions such as ants attending scale insects for honeydew.

In general, the basic natural history of the monsoon invertebrate fauna of northern Australia is too poorly known to assign functional roles to most invertebrates in our samples. Nonetheless, some comments on the ecology of the fauna are noteworthy. The Hymenoptera identified in this study provide a substantial list that is fundamentally different from that recorded from the dwarf mistletoes *Arceuthobium* (Stevens & Hawksworth 1970; Whittaker 1984), with numerous parasitic and mutualistic associates present. For example, the site with Chalcididae, a known endoparasite of Lepidoptera larvae, was the same site that contained a cohort of *Delias* larvae (Pieridae). The wasp families Encyrtidae, Scelionidae, Aphelinidae, Braconidae, Eulophidae, Elasmidae and Bethylidae probably parasitise Miridae and lepidopteran larvae (G. Brown, pers. comm.). Agaonidae are *Ficus* (Moraceae) specialists, but in this study one species was recorded at three different sites, all in flower, with no *Ficus* growing nearby; the appearance of this wasp at more than one site suggests that it was not a transient species. The three species of Tropiduchidae and Cicadellidae (Hemiptera), when present, were recorded in high numbers with all life stages present, indicating evidence of breeding. Among the Lepidoptera, several taxa from the families Pieridae and Lycaenidae are known obligate mistletoe specialists (Braby 2000), and our breeding records for the Immidae and Geometridae have not previously been recorded for the Loranthaceae (see Common 1990 for review of the Australian fauna). Among the Coleoptera, three unidentified species of Curculionidae were recorded each from different sites, but none comprised the ubiquitous mistletoe weevil *Metyrus albicollis* which resembles droppings of the Mistletoe Bird *Dicaeum hirundinaceum* (Shaw). Whittaker (1984) recorded Coccinellidae feeding on aphids (Aphididae) on *Arceuthobium*, but in this study Coccinellidae were sampled at six sites, with aphids present at only two of these. Chrysopidae (Neuroptera) larvae also feed on aphids as well as Cicadellidae, but no aphids or cicadellids were present at the respective sites.

Taxonomic richness was positively related to mistletoe fresh weight, indicating that larger clumps supported higher diversity. In contrast to expectations, there was no effect of host tree on the mistletoe invertebrate fauna. There are two alternative explanations for the lack of a clear host effect. First, the mistletoe invertebrate fauna may be different from that of the host tree with little or no overlap between the two groups; this hypothesis carries the prediction or implication that the mistletoe invertebrate fauna is specialised and independent of its host tree. Second, the mistletoe invertebrate fauna may be similar or even identical to that of the host tree, with the implication that mistletoes support a widespread generalised fauna that is also shared between taxonomically different host trees. Both hypotheses require further testing and comparative analysis, but consideration of the discussion above, host affiliations among the Lepidoptera sampled, and chemical differences among the host tree genera, implies that the first hypothesis is more likely.

In Australia, mistletoes are often considered by local authorities as a weed due to high levels of infestation in non-natural (suburban and semi-rural) landscapes, and are selectively removed by physical or chemical means as part of the eradication process (Minko & Fagg 1989; Fagg 1997). In the NT, for example, the Darwin City Council regards mistletoes as a weed and they currently remove them when they are found, despite the fact that all mistletoes in Australia are native and most are endemic to the continent (Barlow 1984). However, such practices should be discouraged given the importance mistletoes play in the ecosystem as a keystone resource (Watson 2001), the complex ecological interactions they facilitate (Room 1972b; Whittaker 1984; De Baar 1985b) and the wide range of invertebrates that they support, some of which are obligate specialists. In suburban landscapes such as Darwin, it is assumed that mistletoes fulfil a similar ecological role in maintaining local biodiversity. The suburban landscape of Darwin, compared with other capital cities in Australia, is rather unusual in that it has a low population density (c. 114,000 people, including its satellite city Palmerston and the outer rural area, distributed over an area of approximately 926 km^2) and a relatively high proportion of natural vegetation within the urban matrix. In Queensland, the Brisbane City Council has recently begun implementing better practices of mistletoe management in suburban parks and street trees for the maintenance of biodiversity in the urban environment (Moss 2006). These practices include a moratorium on mistletoe removal and the protection of specific host trees that Brisbane residents bring to the Council's attention, and such practices ought to be adopted by other cities.

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Appendix. Data matrix summarising occurrence of taxa across sites.

This appendix may be viewed at:
http://sites.google.com/site/ntfieldnaturalists/home/journal.

Mistletoe invertebrates: left - the day-flying moth *Birthana cleis*; below - a butterfly, the Northern Pencil-blue *Candalides margarita gilberti*. (Michael Braby)

The mistletoe *Decaisnina signata* is common on trees in urban Darwin: below right - with flower buds and a jumping spider, *Cosmophasis* sp. (Salticidae) (Tissa Ratnayeke); below - inflorescence with open flowers (Michael Braby).